## 3. THE LIFE CYCLE IN HEMIPTERA
### (Excl. Aphids and Coccids.)

By E. D. Ball.

The life history of any insect if carefully and conscientiously traced, will show many and striking adaptations. These in the aggregate will be found to display a marvelous adjustment to and harmony with the environment. The life cycle may be long or short, occurring early or late, the generation one or more and the winter passed as egg, nymph or adult, according as these variations adapt the insect to its individual niche in the scheme of things.

In the main these adaptations are not, however, mere adjustments to a temporary excess of heat or cold, moisture or dryness, but rather are deep-seated and fixed modifications brought about through reaction to seasons unnumbered whose means, at least within the limits of the present geological period, are constants. Such adaptations as these are not to be overthrown by the influence of an early season or a late one, a heavy rainfall, or even an arid condition. They are merely modified in detail, but these modifications only serve to emphasize the fixity of the underlying principle. The man who wrote "The number of generations a year will vary in different parts of the country according to the various climates and is likely to fluctuate from year to year in accordance with seasonal variations" was so impressed with trivial details that he entirely missed the great concept of nature's plan whereby each and every species exists as a species primarily because it has through the ages become differentiated and adapted to its humble place in the structure of life. His concept of nature is that of the thistledown blown by the wind while the reality is the majestic elm bending and waving in every passing breeze but which in the end remains firm and upright.

Commencing with the Cicadidæ as probably the lowest type of the field assigned, we find a marked uniformity in their life history in that all the species pass the winter as nymphs and all have an under-ground habitat, coming out as adults with marked uniformity in the middle of the summer. Beyond that, little is known except for one species in which the life cycle requires 17 years and a variety in which this number is reduced to 13. Popular opinion credits the other species with two-year cycles. According to W. T. Davis this originated with Jæger in the "Life of North American Insects" published in 1854 and he credits the information to Pontedera. Whether Pontedera's statement was the result of experiment or only a guess has apparently never been tested. Absolute fixity of the 17 and 13 year cycles is, however, one of the marvels of nature and should be an everlasting refutation of any suggestion that insect activity is subject to fluctuation like the ever changing thistledown.

The CERCOPIDÆ or Frog-hoppers show a marvelous adaptation in their froth making habit and they have apparently depended largely upon this rather than other modifications for their protection. All of our local species have a single annual generation and all but one pass the winter in the egg stage. The variations in this single generation will be discussed under that head in the next family.

The MEMBRACIDÆ or tree-hoppers are celebrated for the wonderful variety and complexity of their adaptations to their food plants. When it comes to the life cycle on which most of these adaptations are based, it is found to be fundamentally very simple. 90 per cent or more of our species have a single annual generation and more than 90 per cent pass the winter in the egg stage. The tree hoppers of the genus *Telamona*, for example, feed very largely on the sap of the trees and mainly on the tender growing twigs. They find optimum conditions for such feeding only during the comparatively short period in which the tree is making its growth. They also must find a location and deposit their eggs while the wood is still soft and tender; otherwise they will be unable to penetrate to a sufficient depth to protect the eggs from predacious and parasitic insects. The result is that we find that they, with a possible exception, pass the winter in the egg stage and have a single annual generation. The overwintering eggs in the twigs hatch almost with the first growth in May. The nymphs mature in June. The adults lay eggs in July and August and the cycle is finished.

In the case of *Ceresa bubalis* (the Buffalo tree-hopper) and its vegetation-feeding allies the need of haste is not so great as their food plants, Composits, Legumes and others, grow all summer, so we find the nymphal period both longer and later and the adults extending into the fall.

A striking adaptation to a special period in a plant's growth, is shown in the life cycle of *Micrutalis calva*, the little shining black seed-like tree-hopper. The nymphs are found between the branches of the blossom head of the Ironweed, *Vernonia*. This purple flower appears only in the fall, so that the single generation of nymphs comes on over 70 days later than its relative that lives in the tree.

Later appearing nymphs usually come from overwintering adults that feed for some time before laying eggs. The complete life cycle of this species is not known. What we do know corresponds with the life cycle of *Publilia* in which we know that the adults hibernate and that there is a single generation on thistles, sunflowers and other late growing *Compositæ*.

The writer has never studied a double brooded tree hopper. Funkhouser, a careful student of the family, has, however, published the details of his observations on *Vanduzea arcuata* which lives on the Black Locust. From the observed facts the writer has been able to construct a complete life history chart showing two generations, with the winter passed in the egg stage.

It is to be regretted that after completing this fine series of observations that Prof. Funkhouser allowed himself to be led astray by the example of that all-too-numerous band of dilettante and superficial workers in Entomology whose chief indoor sport has been the working out of life histories by the mathematical route. The only thing necessary for these scientific wizards is to ascertain the time that it takes an egg to hatch and a nymph to develop, add the two, and divide the length of the season by this number. The quotient is *not* the number of generations nor even the number of *possible* generations of the insect that they fondly imagine it to be, but a mathematical fiasco and a scientific absurdity, patent to anyone who will give the matter serious thought.

If the time of the stages used was a fair average of the season our short-cut investigator will probably find three or four broods. If the minimum time found in the midsummer period alone is used and our rapid calculator is optimistic about the spring and fall weather, as he is usually, then at least 5 or 6 generations will be proclaimed. If our mathematical prodigy would only take the trouble to investigate the literature (which he will not) he would find that no one has ever carried a single species of the higher Homoptera through as many as three complete generations in a season.

There are two fundamental fallacies embodied in all calculations of this kind. The first and most important being that Nature is trying to see how many generations she can produce annually. She is not—in Hemiptera or Orthoptera at least—but rather trying to see how perfectly she can adjust the distribution of the one or two generations to the optimum conditions for development in the variable seasons. The tree hopper might have three generations as far as the time factor was concerned but it can have tender twigs for only one and one it consequently has. The little black *calva* might have three and our mathematical optimist would say four generations but it could not have the rich food destined for the forming seeds in more than one and so it is content with one.

The second common fallacy is that the time from egg to adult is the measure of a generation—it is instead only about half of the period. In the Hemiptera the adult emerges with eggs undeveloped and they must feed and develop them before egg laying begins. Somewhere in this period mating takes place. Funkhouser shows mating 10 or 15 days after the adults appear in *Vanduzea*. Johnson states that the grape leafhopper fed 10 days before mating, Childs shows a longer period for the rose leafhopper, while Fenton and Hartzell show a still longer period for the potato leafhopper before egg laying began. In some cases the mating appears to be near the beginning and in other cases near the end of the period, but in all cases it must of course precede egg laying. The total time therefore between adult emergence and egg laying appears to be from 10 to 25 days.

Hemipterous insects rarely if ever lay all their eggs at one time. Instead the Homoptera as a rule lay a few at a time through long periods. Hodgkiss found *Stictocephala* laying as many as 250 eggs through a two-month period. Johnson found the grape leafhopper laying 115–140 eggs through a 70-day period. Ball found the beet leafhopper laying eggs for two and a half months. Fenton and Hartzell found the potato leafhopper laying eggs for 50 days. In all life history studies made, this period has been shown to be longer than the time required from egg to adult and often two or more times as long. This period, which must be considered as part of the time required for a complete cycle, will amount to from 30 to 70 or more days.

The total time required for the development of a complete generation of a Hemipterous insect will then be made up of the following factors and be somewhere within the limits suggested:

| | Min. | Ave. | Max. |
|---|---|---|---|
| Development of eggs (including mating time)............ | 10 | 17 | 25 |
| Period of egg deposition.................................... | 30 | 50 | 75 |
| Egg Stage................................................ | 10 | 15 | 35 |
| Nymph stage.............................................. | 12 | 30 | 55 |
| | 62 | 112 | 190 |

This tabulation, which is of course merely suggestive, indicates that the minimum time necessary to mature a complete brood is over two months, the average time three and two-thirds months, and that in some cases it requires over six months for the process.

With these facts in mind we may return to Professor Funkhouser's too ready acceptance of the facilities of the mathematical prognosticator and note that the first two of his proposed generations correspond with the beginning and maximum of the first generation according to his own statements and that the remaining two belong in the same way to the second. He found only two mating periods and these correctly.

Wildermuth working in Tempe, Arizona, gave careful and accurate figures on the beginnings of each stage in the life cycle of *Stictocephala festina* and especially increased our knowledge of the effect of temperature upon the rate of development of eggs and nymphs, showing an average variation in egg development from 14 to 35 days and of nymphs for 32 to 68 days. He, however, was led into the common error and after giving detailed figures enabling the writer to chart two definite broods he "calculated" that there were four broods. He did not give figures that would enable one to close up the posterior extensions of the stages with accuracy but the ordinary extension is amply sufficient to explain the presence of all stages late in the season which misled him into the four brood fallacy. The chart is also interesting in showing the wide variations in the time of appearance of insect life in the arid southwest as compared to that in New York. This is especially noticeable when it is remembered that this is a species with an adult hibernation which under ordinary circumstances would tend to throw the first generation later than the one that wintered in the egg stage.

The writer's experience in the arid region and especially in the Imperial Valley indicates that this early starting is an almost uniform adaptation. Insects develop abnormally early in the spring before ordinary temperatures are reached and their life cycle is practically completed before the drying up of the vegetation by the excessive heat of the fall so that only those stages that are developed to resist adverse conditions remain in any numbers. This will be brought out again in the case of the grape leafhopper.

The CICADELLIDÆ or leafhoppers, have more economic species and have received more study than any other family in the group. On the other hand the FULGORIDÆ, called lantern flies, or more commonly leafhoppers have probably received less attention. Both groups of these leafhoppers appear to have about the same variation in their life cycles and will be treated together. These leafhoppers feed on all types of vegetation, trees, shrubs, perennials, biennials, and annuals, under every condition of humidity, moisture, and temperature, and yet the writer has never been able to find a single example in which it could be demonstrated that more than two generations a year occurred nor on the other hand one in which there was less than one generation per season. This is a very limited range and yet, in almost every case investigated, a definite and sufficient reason could be found for the limitation in generations and that reason was almost invariably its adaptation to some period in the growth of its food plant.

The leafhoppers with a single annual generation may be roughly divided into three groups, depending upon whether they pass the winter as eggs, nymphs or adults. In general passing the winter in the egg stage will result in the earliest development in the spring, and in this class we find *Empoasca unicolor*, the real apple leafhopper. This species has been worked out by Lathrop in New York, Brittain, in Nova Scotia, and Fenton in Iowa, and all of them find an early nymphal period in May and June, with adults from that time on throughout the season, egg laying occurring late and these eggs going over winter. This, as explained previously, is the adaptation to the short period of growth of the mature apple tree and is a general type of adaptation found in a large number of tree-infesting leafhoppers such as those found in the family *Bythoscopidæ.*

But a small percentage of the leafhoppers winter in the nymphal stage and when they do it is usually in response to some peculiar adaptation. *Dorycephalus platyrhynchus,* is a remarkable shovel-nosed leafhopper so wonderfully fitted to the stem of the *Elymus* (wild rye), that it is even said to show the rust spots so well that the species of rust can be determined. This species shows an equally remarkable adaptation in its life history. The eggs which are laid through a long period of time, hatch out at the time the flowers appear, and the little alligator-like hoppers waddle their way up the stalk to the head and come to rest flattened out beneath the glumes where they remain and suck out the nutrition intended for the developing seeds. When the seeds mature they pass to the base of the plant and feed on the green sprouts until winter. In the spring they come out and feed again until May when they change to adults, ten or eleven months from the time they left the egg. It would take a mathematician of some ability to figure many generations in a season of this species and it would take a mind of equal ingenuity to devise a more interesting adaptation.

In the old group *Tettigonidæ* the great majority of the species pass the winter in the adult stage and have a single annual generation. *Oncometopia lateralis* is a typical example of this group. In this we see the adults mating and beginning laying eggs in May, continuing until the end of July. The first eggs develop into adults some time before the last of the overwintering brood of adults disappear so that we have adults the year round and nymphs coming on through a period of three or even four or more months. The writer studied this species in Colorado and there the adults that develop, whether early or late, do not become sexually mature until the winter has been passed. The continuous occurrence through such a long period of time has frequently led the mathematical investigator astray. Sanderson working in Texas suggested a possible five generations, while Gibson working in Arizona, with what was probably a two brooded species, announced six.

Turning to the two brooded species of leafhoppers the life history of *Empoa rosæ,* the rose leafhopper, was carefully worked out by Childs in Oregon and shows a beautiful adaptation to the long and even temperature conditions during the growing season of that region. Starting as early as the first leaves appear this species has a generation on rose the adults of which fly to the apple, producing there a second brood which in turn flies back to the rose to deposit eggs to pass the winter.

In sharp contrast with this extended life history period the potato leafhopper *Empoasco mali* as worked out by Lathrop in New York and Fenton and Hartzell in Iowa, shows a very restricted developmental period. The adults hibernate and as usual with such species appear late in the spring, feed on weeds through May, and fly to the potatoes in June. This year they appeared suddenly on potato June 6th, where they laid eggs for nearly two months. The first generation was produced on the early potatoes but the adults did not lay eggs there as they appeared. Instead they waited until after the summer migration which was mostly to the late potatoes and deposited their eggs there for a second generation in the fall. Adults of this generation did not become sexually mature that season. The two periods of development of hopperburn coincided with the development period of the two generations of nymphs. This species has previously been credited with four generations in Minnesota, five in Iowa, while one enthusiast, not to be outdone, announced six for Mississippi, although there is not a single suggestion that any continuous breeding work from generation to generation had been done to verify these preposterous statements. By reference to the charts it will be seen that there would be adults, eggs, and nymphs present on the vines in numbers continuously from the middle of June until frost and this was apparently the only justification for the use of the mathematical method.

The most carefully worked out study of the life history of a leafhopper ever published was made by Fred Johnson on the shores of Lake Erie in 1912. Johnson succeeded in keeping the grape leafhopper, which winters as an adult, alive in cages through the summer and on into September and obtained from 115 to 140 eggs apiece deposited through a period of more than 60 days. He found a single complete generation of nymphs extending from June to October, a period long enough so that three individuals could have successfully matured. Only the very earliest adults of the developing brood appearing in July ever mated and the resulting production of nymphs of a partial second generation was so small as to be almost negligible. Contrasting with this Quayle in California found that this species had two generations and appearing a month and a half earlier, but concluded its development equally early in the fall as is characteristic of the southwest region. The grape leafhopper had, by practically all superficial workers been credited with a considerable number of generations. Slingerland, by careful and thorough work, reduced this to a possible two. Quayle, under the most favorable possible conditions for a continual production of generations, was unable to find any trace of mating or reproduction in the second brood adults. He did not, however, follow his first generations through and it may possibly be that the second generation was not a complete one even in that region.

The writer has shown that in the single brooded beet leafhopper the nymphal period varies from April and May in Arizona to July and August in Idaho, and that there are all gradations in the intervening regions without changing the single brooded condition. This species is adapted to feeding on the plants of the beet family and the single generation appears in a region at the time when the food plant is making its most rapid growth.

The problem of obtaining continuous cage records from generation to generation, with such delicate and active insects as the major portion of the leafhoppers have proved to be, is one of the greatest obstacles to accurate knowledge of this group and no doubt one of the fruitful causes of the mathematical propensity of some of the workers. There are, however, a number of ways of determining what is occurring in the field and in checking up incomplete cage records, even where there is an apparently continuous production of nymphs and adults. The most important single landmark of the season is the mating period. If mating is observed in abundance a new generation will soon follow. This is the time when flights occur, migration takes place, and at this time males often fly to lights in numbers. If on the other hand a great preponderance of females are found it will be the later stages of the egg deposition period. The males are always the first to mature and then there is a short period during which the sexes are equal while the last remnants of a brood of adults are always females. If males and females are abundant and no mating is taking place, superficial dissection of the female will at once show whether eggs are present. In cases of adult hibernation the fall generation does not mate and no eggs develop that season.

In the HETEROPTERA we find a very similar condition with respect to generations. All species have at least one generation a year while few if any have more than two. Adult hibernation is very common in this group, in fact, it is the rule in a large number of families and occurs in nearly all of them. Mating is very conspicuous and takes place through a considerable period, thus giving a guide to the generations. The eggs in a number of groups are deposited on the leaves and are easily observed.

The chinch bug which used to range from northern Wisconsin to Texas, had two annual generations and adult hibernation throughout. Its relative ,the false chinch bug, appears to have a similar life cycle although a recent writer announces four generations. His four broods were mathematically calculated but he naively noted that it was very difficult to obtain nymphs during two of the periods while during the other two they were abundant.